NEW LOWER TERTIARY CRABS FROM PAKISTAN

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ABSTRACT. Palaeocene and Eocene crabs are described from the Sulaiman and Kirthar Ranges of east Pakistan. Ten species are represented, eight of them new, belonging to nine genera, two of them new. The new genera and species are *Hepatiscus sheranii* sp. nov., *Laeviranina sinuosa* sp. nov., *Pyromaia inflata* sp. nov., *Gillcarcinus amphora gen.* et sp. nov., *Proxicarpilius planifrons* gen. et sp. nov., *Proxicarpilius minor* gen. et sp. nov., *Hexapus pinfoldi* sp. nov., and *Lobonotus orientalis* sp. nov.

AMONG the foreign collection of fossil crabs in the Department of Palaeontology, British Museum (Natural History), are three groups from the Palaeocene–Eocene of Pakistan; two, presented by E. S. Pinfold (1938) and T. O. Morris (1934), come from the Ghazij Formation of Dera Ghazi Khan District and Kalchis respectively, while the third and largest group comes from the Kirthar Formation of North West Frontier Province and was presented by Professor W. D. Gill and B. C. M. Butler in 1958.

The first reference to crabs from the Eocene of the Indian Sub-Continent was communicated by d'Archiac and Haime in 1854, with the description of *Arges Murchisoni* (= *Galenopsis murchisoni* A. Milne-Edwards). Stoliczka (1871) advanced the knowledge of the Eocene crab fauna with the description of *Palaeocarpilius simplex*. Subsequently Withers (1932) and Glaessner (1933) have either described new species or correlated them with others from European deposits. Sastry and Mathur (1970) completely reviewed the entire decapod fauna of this region and included stratigraphical tables as well as an extensive bibliography.

The new material forms an aggregate of some 272 specimens. From the Ranikot and Ghazij Formations *Glyphithyreus wetherelli* (Bell) has been distinguished, together with three new species, one of which is contained in the oxyrhynch genus *Pyromaia*; the others belong to *Laeviranina* and *Lobonotus*. Six more species are present from two horizons, known locally as the Drazinda Shale and Domanda Shale, within the Kirthar Formation. One species, *Lobocarcinus indicus* Glaessner is known by specimens of similar age from Baluchistan; the others are new and are referable to *Hepatiscus*, *Hexapus*, and two new genera *Proxicarpilius* and *Gillcarcinus*.

STRATIGRAPHY

The Ghazij Formation, formerly Ghazij Group of Oldham (1890), lies above the Dunghan Limestone (Upper Cretaceous to Lower Eocene) and below the Kirthar Formation (Middle Eocene to Oligocene). The age of the Ghazij Formation has been assessed as Lower Lutetian by Vredenberg (1909), but most authors including Iqbal (1970*a*), conclude that both the micro- and macro-palaeontological evidence suggests

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a correlation with the Laki Group, regarded by Cox (1931) on the basis of its molluscan fauna, as Lower Eocene (Ypresian). However, Haque (1960), on the basis of the smaller planktonic foraminifera of the Sor Range, considered the upper part of Ghazij Shales to be middle to late Eocene in age. In this assessment of the age of the Ghazij Formation, Haque is alone, although Hunting Survey Corporation Ltd. (1961, 124) thought a few samples from near the base of the formation contained fossils considered to be of Palaeocene age or at least of Palaeocene affinity. To date the most authoritative statement on the age of the Ghazij Formation is Samanta (1972), who suggests that the Ghazij Formation lies wholly within the Lower Eocene planktonic foraminiferal Zones *Globorotalia aspensis/esnaensis* and is probably equivalent to Bolli's (1957) Zones of *G. aragonensis* (P8) and *G. palmerae* (P9). In the East Indian Letter classification it is assigned to Ta_2 (Adams 1970). The formation has a thickness of 300 m (min.) to 3000 m (max.) in the Sulaiman Range (Hunting Surveys 1961) and consists principally of shales with subordinate beds of sandstone, limestones, conglomerates, and thin coals (Iqbal 1970*a*). Kasi (1968), who studied the sedimentology of the Ghazij Formation at Harnai, divided the section into four lithological divisions. Unfortunately it is not known from which of these divisions the crabs were obtained, but the nature of their preservation suggests that they were not all found at the same level. In the summary, Kasi concludes that the sediments were formed in marine and fluviatile environments but that there is no evidence despite the presence of coal in the sequence to suggest that any deltaic sediments are present. Hunting Surveys (1961) discussed the possible derivation of the sediments. Iqbal (1970*a*) considered that the macrofauna of the Ghazij Formation is typically marine and probably lived in the littoral to sublittoral zone of a warm sea 45 to 60 m deep. Clear water is indicated in at least one subdivision by the presence of corals, but the molluscs in other subdivisions suggest phases of a shallower muddy-water environment. A number of the molluscs recorded are long-ranged and some appear in contemporary and later (Lutetian) European deposits. Iqbal concluded his summary of the molluscan assemblage by saying, 'There is no evidence that the species common to West Pakistan and Europe appeared first in this part of Pakistan and migrated towards Europe during Eocene times.' The presence of *Glyphithyreus wetherelli* (Bell) (Withers *in* Davies and Pinfold 1937) in the Thanetian, Upper Ranikot Formation, Patala Shales of Kalabagh does not in any way contradict this conclusion, since the Tethys was open along its length during this period. British and west European rocks of Thanetian age are unsuitable for the preservation of crabs, so that absence of *G. wetherelli* from the European Palaeocene cannot be used as evidence for a westerly migration.

The Kirthar Formation (Middle Eocene to ?Oligocene) overlies the Ghazij Formation and has been discussed at length by Eames (1952). Of the crabs from Ramak Kwar, *Gillcarcinus*, *Lobocarcinus*, and *Proxicarpilius* were found approximately 90 m from the top of the Domanda Shale (Iqbal 1970*b*) and are equivalent to the Lower Chocolate Clays recorded by Eames (1952). *Hexapus* and *Proxicarpilius* were obtained from the *Discocyclina* Shales (= lower part of the Drazinda Shale) which according to Gill succeeds the *Ostrea* Shales (= Domanda Shale) after an intervening limestone and is approximately 210 m above the main crab horizon.

The Lower Chocolate Clays consist of chocolate-coloured reddish-brown and

greenish gypseous shales with some stringers of sulphurous material, limonitic concretions, and phosphatic nodules. Thin bands of impure limestone containing *Ostrea* (*Liostrea*) *pseudoflemingi* Eames occur in the upper part of this group (Eames 1952). Gill (*in lit.*) says, 'crabs have been found at about the same horizon over about 20 miles (32 km) or more over the outcrop [i.e. Ramak Kwar and Parwara]. In some cases they occur in association with sandy beds crowded with molluscs, obviously a shoreline facies. Some of the best preserved crabs undoubtedly came from the greenish shales between the sandstone.' Eames (1952) places the Upper and Lower Chocolate Clays in the Lutetian Kirthar Formation. In his summaries of the palaeontological subdivisions Eames (1952) refers to up to six decapod species from the Rakhi Nala section and five each from the Zinda Pir and Kohat sections. Unfortunately these species are not named and since the complete faunal lists mentioned by Eames cannot now be traced, no correlations can be made with the present material. The only named decapod is a *Callianassa* sp. from the *Venericardia* Shales (Local Zone 1 of the Rakhi Nala section).

DISTRIBUTION

Of the six species listed by Glaessner (1933) from the Lutetian of the Indian Sub-Continent only *Lobocarcinus indicus* Glaessner and *Galenopsis* cf. *murchisoni* have been recorded from Europe; *L. indicus* is also known from Egypt and possibly Senegal and Panama (Via 1969). *Palaeocarpilius macrochelus* (Desmarest), included in Sastry and Mathur's (1970) faunal list of Lutetian species, is well represented in deposits of similar age from Europe and elsewhere. When the distribution of the five genera concerned is considered, only *Goniocypoda* from the Maastrichtian of Senegal (Remy 1954) and *Lophoranina* from the Lower-Middle Eocene of Indonesia (Via 1969) are known from older deposits.

Among the genera and species in the new material from the Ranikot and Ghazij Formations (Thanetian-Ypresian), *Glyphithyreus wetherelli* (Bell) is known from the Ypresian deposits in England, north-east Europe, Spain, and Senegal; *Laeviranina* is known from Lower, Middle, and Upper Eocene of Europe and Middle and Upper Eocene of the U.S.A. and New Zealand; *Lobonotus*, on the other hand, is known only from the Middle Miocene of North America, while *Pyromaia*, a Recent North American genus containing only three species, has previously only been found fossil in the Pleistocene of California.

From the Kirthar Formation (Lutetian), *Hexapus* hitherto known only from Miocene, Plio-Pleistocene, and Recent species, appears to be essentially Indo-Pacific in distribution, while *Hepatiscus* is represented by contemporary and younger species from Europe, Egypt, Venezuela, Java, and the U.S.A.

TABLE 1. Crabs recorded from the Palaeocene and Eocene of Pakistan and neighbouring India.

	Palaeocene	Ypresian	Lutetian: Domanda Shale	Lutetian: Drazinda Shale	Lutetian: Undifferentiated
**Glyphithyreus wetherelli*	+				
Goniocypoda rajasthanica	+				
**Laeviranina sinuosa*		+			
**Lobonotus orientalis*		+			
**Pyromaia inflata*		+			
**Lobocarcinus indicus*			+		+
**Hepatiscus sheranii*			+		
**Gillcarcinus amphora*			+		
**Proxicarpilius planifrons*				+	
**Proxicarpilius minor*				+	
**Hexapus pinfoldi*				+	
Lophoranina bakeri					+
Montezumella sp.					+
Lobonotus sp.					+
Palaeocarpilius macrochelus					+
Palaeocarpilius simplex					+
Galenopsis murchisoni					+
Galenopsis cf. *typicus*					+
Goniocypoda sindensis					+

* This paper (others from Sastry and Mathur 1970).

SYSTEMATIC PALAEONTOLOGY

Section OXYSTOMATA H. Milne Edwards, 1834
Family CALAPPIDAE de Haan, 1833
Subfamily MATUTINAE McLeay, 1838
Genus HEPATISCUS Bittner, 1875

Type species. Hepatiscus neumayri Bittner, 1875, subsequent designation by Glaessner 1929.

Range. Lower Eocene to Oligocene.

Hepatiscus sheranii sp. nov.

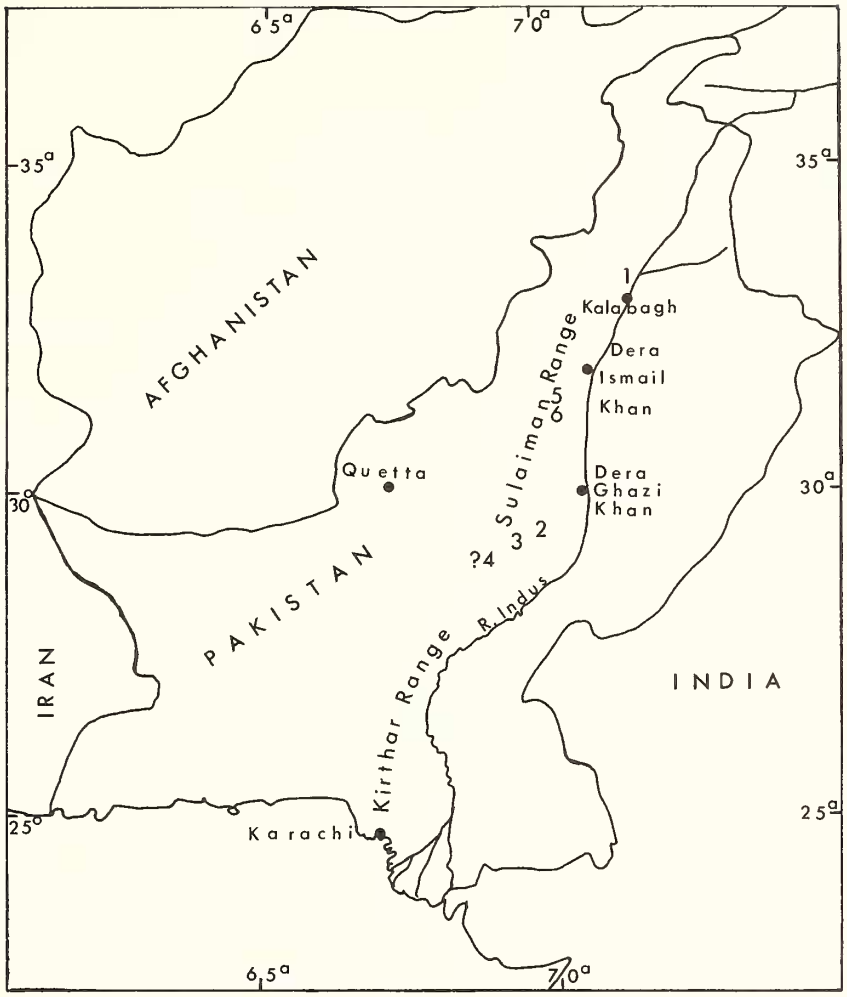
Plate 116, figs. 1–3

Derivation of name. From Sherani, a local tribal name.

Diagnosis. Carapace subhexagonal in outline with the front raised up; the regions are well defined and nodulate.

Material. Two, part cast, part decorticated carapaces. Holotype, male, In. 61551. Paratype, female, In. 61552.

Horizon and locality. Middle Eocene, Domanda Shale, Kirthar Formation; Ramak Kwar; *c.* 85 km south-west of Dera Ismail Khan, North West Frontier Province, Pakistan.



TEXT-FIG. 1. Sketch map of Pakistan showing fossil localities 1–6.

Locality 1. Ranikot Formation, Patala Shale, Thanetian Stage; 3 km north of Kalabagh, 160 km north-north-east of Dera Ismail Khan, Punjab Province, 32° 51′ N., 71° 36′ E.

Locality 2. Ghazij Formation, Ypresian Stage; south of Nila Kund, 100 km south-west of Dera Ghazi Khan, Punjab Province, 29° 30′ N., 69° 45′ E.

Locality 3. Top of Ghazij Formation, Ypresian Stage; Shaisuro, Mazari tribal area, *c.* 150 km south-west of Dera Ghazi Khan, Punjab Province, 28° 55′ N., 69° 50′ E.

Locality 4. Ghazij Formation, Ypresian Stage; Kalchis, Baluchistan Province (exact location not established but probably in the Kirthar Range).

Locality 5. Kirthar Formation (= Brahui Limestone, Kirthar Member), Domanda Shale (*syn.* Lower Chocolate Clays), Lutetian Stage; Ramak Kwar (river), *c.* 85 km south-west of Dera Ismail Khan, North West Frontier Province, 31° 27′ N., 70° 20′ E.

Locality 6. Kirthar Formation, lower part of Drazinda Shale (*syn.* Upper Chocolate Clays), Lutetian Stage; south of Parwara village, 9 km south-west of Domanda, North West Frontier Province, 31° 32′ N., 70° 09′ E.

Description. The carapace is subhexagonal in outline with the width slightly exceeding the length; it is moderately rounded transversely and semi-elliptical in longitudinal section. The anterolateral margins are convex and the edge at the broadly rounded lateral angle is thickened and upturned. Somewhat sinuous posterolateral margins converge abruptly to the narrow posterior margin; it is rather more deeply concave in the male; and is about half the width of the orbitofrontal margin. The orbitofrontal margin occupies about half the carapace width and is raised a little above the level of the lateral margin; the front is not well preserved, but appears to have a median cleft. The orbits are wide and ovate; the lower orbital margin is produced a little in advance of the upper which is thickened and apparently without notches. The basal segment of the antennules takes up a third of the orbito-antennular cavity and on either side of the short epistome, small lunate cavities for the second segment of the antenna open into the orbit. On the dorsal surface the regions are well differentiated and nodes of more or less even size occupy the proto- and mesogastric lobes, cardiac region, and epibranchial lobes; while that on the metabranchial lobe is smaller and set close to the margin midway between the lateral and posterior angles; an obscure node is set in the depression between the mesobranchial and cardiac nodes. The parallel-sided anterior process of the mesogastric lobe is depressed and does not reach the front. A shallow groove, rather more obvious than the cervical groove, separates the hepatic regions from the protogastric lobes. The urogastric lobe is depressed and confluent with the rounded cardiac region.

A subsurface shell layer shows the dorsal surface densely pitted, the pits becoming finer to obsolete towards the posterior margin.

The 3rd maxillipeds are fragmentary, but show the exognath to be about half the width of the endognath.

The 1st and 2nd thoracic sternites are diamond-shaped and delineated by a groove from the 3rd sternites which in turn are separated by a groove, notched at the margin, from the 4th sternites. In the male this groove passes round the tip of the abdominal trough and the median portion of the 3rd sternite is depressed, but in the female the tip of the abdominal trough is wide and extends nearly the whole length of the 3rd sternite. The posterior margins of the 4th–6th sternites partially overlap the succeeding member; the 4th and 5th have a low median ridge. The very narrow abdominal trough of the male is deep and sternal grooves issue forwards from between the 6th and 7th sternites. Of the female abdomen, only a subquadrate 6th somite and triangular telson of almost equal length are preserved.

EXPLANATION OF PLATE 116

Figs. 1–3. *Hepatiscus sheranii* sp. nov. Middle Eocene, Kirthar Formation; Ramak Kwar. Dorsal, ventral, and left lateral views of holotype carapace, BM In. 61551. ×2·1.

Figs. 4–6. *Laeviranina sinuosa* sp. nov. Lower Eocene, Ghazij Formation; Nila Kund. Left lateral, dorsal, and ventral views of holotype, BM In. 48241, ×1·5.

Figs. 7–9. *Pyromaia inflata* sp. nov. Lower Eocene, Ghazij Formation; Nila Kund. Dorsal, ventral, and right lateral views of holotype carapace, BM In. 48246, ×3.

Figs. 10, 11. *Lobonotus orientalis* sp. nov. Lower Eocene, Ghazij Formation; Nila Kund. Anterior and dorsal views of holotype carapace, BM In. 48245, ×1·5.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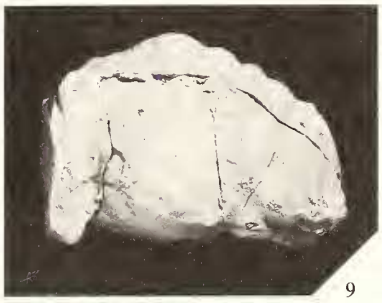
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COLLINS and MORRIS, Lower Tertiary Crabs

Discussion. With the exception of *H. rathbunae* Maury which ranges into the Oligocene (Via 1969), *Hepatiscus* is essentially an Eocene genus and is widely distributed, with species known from southern Europe, Egypt, North and South America, and Java, as well as Pakistan.

The fragment of *H. americanus* Rathbun (1935, pl. 17) shows the arrangement of the nodes to be basically similar to *H. sheranii*, but in *H. americanus* an obscure node occurs between those on the epibranchial and cardiac lobes rather than between the mesobranchial and cardiac lobes. *H. sheranii* differs from all other species of *Hepatiscus* by its rounded outline with unexcavated ventrolateral margins. In addition, *H. rathbunae* and *H. pulchellus* Bittner, have strongly produced fronts and *H. pulchellus* and *H. schweinfurthi* Noetling, have denticulate or spiny anterolateral margins.

Superfamily RANINOIDEA de Haan, 1841
Family RANINIDAE de Haan, 1841
Genus LAEVIRANINA Lörenthey and Beurlen, 1929

Type species. Ranina budapestinensis Lörenthey, 1898, subsequent designation by Glaessner 1929.

Range. Eocene–Oligocene.

Laeviranina sinuosa sp. nov.

Plate 116, figs. 4–6

Derivation of name. From the sinuous course of the frontal ridge.

Diagnosis. A *Laeviranina* with the anterolateral spine immediately behind a sinuous post-frontal ridge, and weak cardiac furrows.

Material. Eleven carapaces: holotype, In. 48241; paratypes, In. 35664–35668, In. 48239, 40, In. 48242–48244.

Locality and horizon. Lower Eocene, Ghazij Formation; Nila Kund, Dera Ghazi Khan District (29° 30′ N., 69° 45′ E.), Punjab, Pakistan.

Description. Carapace about one and a half times as long as wide, moderately convex transversely and longitudinally; it is slightly convex from the front to the level of the cardiac region where it becomes more steeply inclined to the posterior margin. Elongate ovoid orbits occupy the outer fourths of the nearly straight orbitofrontal margin which is about two-thirds of the carapace width. The orbital notches extend half-way to the frontal ridge and apparently divide the upper orbital margin evenly into three portions. Details of the front are not preserved. The anterolateral margin is directed slightly outward, ending with the lateral spine; while broken off on all the present specimens it appears by its basal scar to have been of moderate size and directed slightly upwards; it is situated about the same distance from the external orbital spine as from the widest part of the carapace. The anterolateral edge is narrowly rounded and lined with a row of fine granules which continue along the gently sinuous posterolateral margins and possibly also line the posterior margin. The posterolateral angles are broadly rounded; the concave posterior margin is some two-thirds the width of the front. A postfrontal ridge, concave medially and laterally sinuous, extends across the carapace immediately in front of the lateral

spines; anterior to and along the forward edge of the ridge the surface is crowded with numerous granules of several diameters. A portion of the outer shell-layer (In. 35665) is densely ornamented with minute, rounded pits, but subsurface layers are finely granulated. A pair of deep gastric pits are set between the anterior extremities of short, shallow, cardiac furrows situated close to the midline.

The lateral margin is deflected under at about 45°; the prominent lateral suture is lined with granules and the pterygostomian process is tumid. The buccal cavity appears to have been rectangular, and posteriorly there are deep excavations for the articulation of the 3rd maxillipeds. The portion of the sternum preserved shows it to be broad between the chelipeds and bases of the 2nd pereiopods, and deeply clefted medially as far as the 4th/5th sternal suture.

Discussion. The proportions of the carapace and the anterior position of the lateral spine qualifies this species for *Laeviranina*; the greater relative width of the carapace serves to distinguish it from *Raninoides*. The presence or absence of the postfrontal ridge and cardiac furrows are among the determining characters of *Laeviranina* species; in the type species, *L. budapestinensis* Lörenthey, the postfrontal ridge is situated immediately behind the lateral spine, and in the other three species, *L. glabra* (H. Woodward), *L. fabianii* Lörenthey, and *L. gottschei* (J. Böhm), known to have this ridge, it passes in a fairly even curve across the carapace.

Section OXYRHYNCHA Latreille, 1803
Family MAJIDAE Samouelle, 1819
Subfamily INACHINAE McLeay, 1838
Genus PYROMAIA Stimpson, 1871

Range. Lower Eocene to Recent.

Type species. Pyromaia cuspidata Stimpson, 1871 by monotypy.

Remarks. Previously, *Pyromaia* had only been recorded as a fossil from the Pleistocene of California (Rathbun 1926). Otherwise this genus is confined to the Recent seas around North America.

With the exception of some claw fragments from the Upper Cretaceous of Arkansas dubiously placed in *Stenocionops* (Rathbun 1935) nothing is known of the Oxyrhyncha before the Eocene (Glaessner 1969). An ancestry through the Oxystomata and *Latreillia*—formerly placed in the Homoloidea, but now assigned to the family Latreilliidae within the Dromiacea (Glaessner 1930; Wright and Collins 1972)—has been suggested (Glaessner 1969, R 440). In further support of a dromiacean origin, the marked resemblance of the species described below to *Rathbunopon* (particularly *R. woodsi* Withers) from the Upper Cretaceous of England and the U.S.A. cannot be overlooked.

Pyromaia inflata sp. nov.

Plate 116, figs. 7–9

Derivation of name. From the inflated appearance of the regions.

Material. An almost entire female carapace. Holotype, In. 48246.

Horizon and locality. Lower Eocene, Ghazij Formation; south of Nila Kund, Dera Ghazi Khan, Punjab Province, Pakistan, 29° 30′ N., 69° 45′ E.

Description. The carapace is subhexagonal in outline, the length slightly exceeding the width with the widest part situated at the posterior third. It is slightly convex transversely and in longitudinal section it rises steeply in front, then becoming flatter it continues to rise to the cardiac region before descending sharply to the posterior margin. The frontal margin occupies about a half of the carapace width and is produced slightly beyond the exceedingly shallow, almost circular, forwardly directed 'orbits'. The upper orbital margin is thin and entire; broken bases of the postorbital spines suggest they were stout and directed almost straight forward, basal scars of the pre-orbital spines indicate they were somewhat less robust. The anterolateral margin is very short, rounded, and occupied almost entirely by a large tubercle on the hepatic region. A thin ridge lines the broadly convex posterolateral margin and continues round shallow incisions for the 5th coxae and the very narrow posterior margin. The cervical furrow is shallow and broadly V-shaped where it crosses the midline a little anterior to half the carapace length; turning sharply forward it passes in a broad curve round the mesobranchial lobe to a shallow marginal notch and continues beneath the hepatic lobe to the front. There is a small tubercle on the subhepatic lobe, below and posterior to the hepatic tubercle. The regions and lobes are tumid and in addition to the tubercle on the hepatic lobe there are two small ones on each protogastric lobe forming a convex row level with the tip of the anterior process of the mesogastric lobe. There is a large tubercle on the broadly ovate mesogastric lobe, two on the cardiac region, of which the posterior one forms much the largest on the carapace; three occur on the more or less confluent epi- and mesobranchial lobes, while on the metabranchial lobe there is a tubercle close to the mesobranchial lobe and another, larger one on the outer posterior angle, level with the hindmost cardiac tubercle. A row of three or four very small tubercles leads from the cervical notch on to the outer edge of the metabranchial lobe which overhangs the posterolateral margin. The urogastric lobe is reduced to a narrow bar with a low tubercle on either side of the midline. The intestinal lobe is reduced, barely separated from the cardiac region and bordered behind by a ridge. The branchiocardiac furrow is broader and shallower than the cervical, from the marginal notch it passes obliquely back to become obsolete between the metabranchial tubercles. The elevated portions of the upper surface are densely covered with fine granules which become coarser and sparser in the furrows and between the depressions of the larger tubercles.

The pterygostomian process is triangular and deflected almost at right angles to the lateral edge; a large tubercle lies along the lateral edge and a strong ridge, bearing a single row of fine pits, borders the almost straight buccal margin. A short notch separates the 1st–3rd from the 4th sternites; the notches separating the other sternites terminate in pits and become progressively longer to the 6th/7th where they meet at the midline. The oviducts open close to the midline on the anterior part of the 6th sternites.

Discussion. In the outline of the carapace, the inflated regions and general arrangement of the tubercles, the new species closely resembles *Eoinachoides senni* Van Straelen, from the Upper Eocene of Venezuela, from which it differs chiefly in having

weaker branchiocardiac furrows and a pair of longitudinally, not transversely arranged tubercles on the cardiac region.

Section CANCRIDEA Latreille, 1803
Family CANCRIDAE Latreille, 1803
Subfamily LOBOCARCININAE Beurlen, 1930
Genus LOBOCARCINUS Reuss, 1857

Type species. Cancer paulinowuerttembergensis von Meyer, 1847 by original designation.

Range. Middle to Upper Eocene.

Lobocarcinus indicus Glaessner, 1933

1933 *Lobocarcinus indicus* Glaessner; p. 14, pl. 3, figs. 6, 7; pl. 4, fig. 1.
1969 *Lobocarcinus indicus* Glaessner; Via, p. 390.
1970 *Lobocarcinus indicus* Glaessner; Sastry and Mathur, p. 41, pl. 7, figs. 2–4.

Range. Middle Eocene.

Horizon and locality. Middle Eocene, Kirthar Formation Domanda Shale; Ramak Kwar, *c.* 85 km south-west of Dera Ismail Khan, North West Frontier Province, Pakistan.

Remarks. The only specimen (In. 61668) present comprises the median portion of a carapace; it conforms—as far as the poor state of preservation allows comparison—reasonably well with the type, In. 28125, which comes from a similar horizon at Dera Bugti Khan, Baluchistan.

Section BRACHYRHYNCHA Borradaile, 1907
Superfamily XANTHOIDEA Dana, 1851
Family XANTHIDAE Dana, 1851
Genus GILLCARCINUS gen. nov.

Type species. Gillcarcinus amphora sp. nov.

Discussion. Gillcarcinus has been placed in the Xanthidae rather than in the Goneplacidae because the third abdominal segment of the male does not cover the space between the last pair of ambulatory legs. Other xanthid characters displayed are the notched front, two anterolateral spines, and the front and orbits occupying the entire anterior margin. However, the last character is also common amongst goneplacids, as are the long chelipeds. The mesobranchial ridges and the greatest width occurring in the posterior third of the carapace of *Gillcarcinus* set it apart from all known genera.

Range. Middle Eocene.

Gillcarcinus amphora sp. nov.

Plate 117, figs. 2–4

Derivation of name. The trivial name refers to the large urn-shaped cardiac region.

Diagnosis. The carapace is subquadrate in outline; the antero-lateral margins are of moderate length, convex, and with two small spines; a prominent ridge across the mesogastric and mesobranchial lobes unites with a thin longitudinal ridge on each

metabranchial lobe; the cardiac region is large. Third–fifth somites of male abdomen fused.

Material. Twenty-two carapaces, some retaining parts of the chelipeds. Holotype, a female, In. 61553. Paratypes, 9 males, In. 61554–61562; 4 females, In. 61563–61566; 8 sex indeterminate, In. 61567–61574.

Horizon and locality. Middle Eocene, Kirthar Formation, Domanda Shale; Ramak Kwar, *c.* 85 km south-west of Dera Ismail Khan, North West Frontier Province, Pakistan.

Description. The carapace is subquadrate in outline, the length being about two-thirds of the greatest width; it is moderately convex transversely, and longitudinally it rises steeply from the front to the mesogastric lobe, becomes flatly depressed to the cardiac region before curving steeply down to the posterior margin. The short, almost straight, anterolateral margin ends in a small spine at an exceedingly weak cervical notch and there is a stronger, upturned spine on the epibranchial lobe. The lateral margins are straight and diverge posteriorly to broadly rounded posterolateral angles and lead by wide, shallow incisions for the 5th coxae into the posterior margin which is slightly concave and narrower than the orbitofrontal margin. The lateral edges are drawn up into a thin granulated ridge and the sides are inclined almost at right angles. The straight orbitofrontal margin occupies half the carapace width and is divided into three more or less even portions; the front is a little produced and has a shallow median notch. The upper orbital margin is sinuous, lined with fine granules (continuing round the front) and terminates externally in a blunt spine not reaching as far as the front. The eyestalk (Pl. 117, fig. 4) is circular in cross-section, somewhat constricted medially with the surface minutely pitted; the corneal surface appears to have been directed obliquely upward. On the dorsal surface a strong, rounded ridge crosses the mesogastric lobe and with little or no interruption for the cervical groove continues downwards across the mesobranchial lobes to unite with a weaker, longitudinal ridge on the metabranchial lobes, extending to the coxigeal incisions. A very short epibranchial ridge slopes posteriorly from the lateral margin to the junction of the foregoing ridges. The cervical groove is very faint throughout its course; posterior to the gastric ridge it crosses the midline in a broad curve. In many of the specimens the median portion of the groove is obscure and the hinder part of the mesogastric and normally crescent-shaped urogastric lobe appears as an undifferentiated quadrate area. The anterior process of the mesogastric lobe forms a short depressed triangle between small ovate frontal lobes. A broadly V-shaped groove, more distinct than the cervical groove, separates the urogastric from the

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EXPLANATION OF PLATE 117

Fig. 1. *Lobonotus orientalis* sp. nov. Lower Eocene, Ghazij Formation; Nila Kund. Ventral view of holotype carapace, BM In. 48245, × 1·5.

Figs. 2–4. *Gillcarcinus amphora* gen. et sp. nov. Middle Eocene, Kirthar Formation; Ramak Kwar. 2, ventral view of male carapace with right cheliped, BM In. 61554, × 2·1. 3, dorsal view of holotype carapace, BM In. 61553, × 2·1. 4, anterior view of carapace to show eyestalks, BM In. 61555, × 2·1.

Figs. 5, 7. *Proxicarpilius planifrons* gen. et sp. nov. Middle Eocene, Kirthar Formation; Ramak Kwar. Dorsal and ventral views of holotype female carapace, BM In. 61575, × 1·5.

Figs. 6, 8, 9. *Proxicarpilius minor* gen. et sp. nov. Middle Eocene, Kirthar Formation; Parwara. Dorsal, anterior and ventral views of holotype carapace, BM In. 61647, × 3.


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COLLINS and MORRIS, Lower Tertiary Crabs

cardiac region and there are two small pits set close to the midline. The cardiac region is large, tumid, and urn-shaped. A ridge-like process on each metabranchial lobe above the broadest part and to some extent continuing on to the cardiac region emphasizes deep epimeral adductor muscle scars. The metabranchial lobes are tumid medially to the longitudinal ridge, then become hollowed and steeply inclined to the lateral margin.

Granules of several diameters crowd the gastric ridge and line the metabranchial ones, the tumid areas are less densely granulated, while the depressed median and lateral portions are almost smooth; the area immediately behind the front is finely pitted, with a few granules scattered towards the margins.

Oblique grooves uniting at the midline separate the 3rd from the 4th abdominal sternites; the 4th is nearly square in outline and the 5th–8th are oblong. Granules cluster round the bases of the 4th sternites and there is a row along the adjacent margins of the 5th–8th. In the male abdomen, weak grooves indicate the otherwise fused 3rd–5th somites; the sixth somite is quadrate and nearly as long as the telson. The abdominal trough of a possible male (In. 61556) is deep with a prominent central groove. In the female the 6th somite is about twice as long as the 3rd–5th which are all much the same length. In both sexes the median portion is bluntly ridged and the telson is triangular in outline, but in the male the lateral margins are concave.

The chelipeds are robust and of about the same size on either side; the chelae are equal to about three-fourths of the carapace width. The hand is ovate in section and as long as the downwardly and inwardly curving fingers. There are two grooves lined with pits along the outer margin of the movable finger and one groove along the fixed finger. The carpus is about half the length of the merus which is about half the length of the hand.

Genus *Lobonotus* A. Milne-Edwards, 1864
(= *Archaeopilumnus* Rathbun, 1919)

Type species. *L. sculptus* A. Milne-Edwards, 1864 by original designation.

Range. Lower Eocene to Upper Miocene.

Discussion. *Lobonotus* and *Titanocarcinus* were erected by A. Milne-Edwards (1864) for respectively a Central American and a European species. The two types of areolation that characterize the two genera are not consistent with the apparent geographical separation as at present accepted, i.e. *Titanocarcinus* for Europe and *Lobonotus* for the rest of the world. The characteristic tri-lobed cardiac of *Titanocarcinus* is present on the type species of *Lobonotus*, *L. sculptus*. Examination of the type species of these two genera is required, but it seems likely that *Lobonotus* may become a junior subjective synonym of *Titanocarcinus*.

Lobonotus orientalis sp. nov.

Plate 116, figs. 10, 11; Plate 117, fig. 1

Diagnosis. A *Lobonotus* with the mesogastric lobe divided posteriorly by a weak furrow; the epibranchial lobes are divided laterally by a shallow depression and the intestinal region extends across the entire width of the posterior margin.

Holotype. An almost complete carapace, In. 48245.

Horizon and locality. Lower Eocene, Ghazij Formation; south of Nila Kund, Dera Ghazi Khan, 29° 30′ N., 69° 45′ E., Punjab Province, Pakistan.

Description. The carapace is subquadrate in outline with the width slightly exceeding the length, it is transversely and longitudinally flattened. The orbitofrontal margin is broadly rounded and occupies two-thirds of the carapace width. The orbits are small and ovate. The subtruncate front has a wide, U-shaped median notch and is separated by a shallower notch from the upper orbital margin. The external orbital spine is spiniform; the upper orbital margin has two broad fissures and is lined with granules which continue across the front, those on either side of the median notch being the largest. There are four sharply upturned spines on the somewhat arcuate anterolateral margin; the third spine is the largest, and, while the spaces between the spines are obscured, it is evident that the posterior margin of the fourth is finely granulated. The posterolateral margins are nearly straight and converge to the posterior margin which is about as wide as the orbitofrontal margin. The regions are well differentiated and tumid; the mesogastric lobe is broadly ovate and divided posteriorly by a weak longitudinal furrow, the anterior process extends to the base of small, ovate, epigastric lobes; the protogastric lobes are kidney-shaped and the fairly large hepatic regions are triangular. A thin furrow separates the depressed, rectangular urogastric from the mesogastric lobe. The cardiac lobe forms a large ovate region on which a pair of oblique tubercles coalesce posteriorly; on either side, a small node occupies the space between this region and the metabranchial lobe. The epibranchial lobes are obliquely ovate, with a wide depression laterally. The mesobranchial lobes are small, pyriform, and set close to the urogastric lobes. The intestinal region is narrow and extends obliquely from the posterior margin of each metabranchial round the base of the cardiac. Even-sized granules crowd the summits of all the regions; there is a single row of four or five granules across the urogastric and a similar number on the mesogastric lobe reaches a short way on to the otherwise smooth anterior process.

A thin ridge separates the granulated subhepatic region from the triangular pterygostomian process, on which fine granules follow the subhepatic and sternal margins; and a sharper ridge bounds the slightly concave buccal margin and narrowly rounded buccal angle.

The portion of the sternum equivalent to the 2nd/3rd sternites is laterally tumid and granulated; the 4th sternites are smooth apart from a single row of granules laterally and a few near the margin with the 5th sternites, which, like the 6th–8th, are subrectangular in outline and generally granulated. The merus of the cheliped is a little under half the carapace width in length, robust, and granules of several diameters crowd the lower margin; the merus of the 1st pereiopod is somewhat longer and flattened, fine granules line the upper margin, and coarser ones occur posteriorly.

Discussion. With the exception of *L. foerstei* described by Rathbun from the Upper Miocene of Massachusetts and *L. sculptus* from the Upper Oligocene of Haiti, *Lobonotus* is predominantly an Eocene genus, which hitherto has been known by three species from the U.S.A., one from Mexico, and another, *L.? australis* Fritsch, from Borneo. The epibranchial lobes of *L. natchitochensis* Stenzel (Middle Eocene,

Louisiana) are divided only by a short groove and may be further distinguished from *L. orientalis* in having triangular, not reniform, protogastric lobes, an entire mesogastric lobe, a more distinctly trilobate cardiac region, and coarser surface granulation. The mesogastric lobe of *L. bakeri* (Rathbun) from the Upper Eocene of Texas is also entire, the protogastric lobes are triangular and the epibranchial and mesobranchial lobes are relatively larger than those of the new species. *L. brasoensis* from the Middle Eocene of Texas is known only from a claw fragment. The upper Eocene *L. mexicanus* Rathbun closely approximates *L. orientalis*, but differs in having larger mesobranchial lobes, a more elongate cardiac region, and in the intestinal being much depressed below the cardiac region.

Family CARPILIIDAE Ortmann, 1894
Genus PROXICARPILIUS gen. nov.

Type species. Proxicarpilius planifrons sp. nov.

Derivation of name. Akin to *Carpilius.*

Range. Middle Eocene.

Diagnosis. Carapace transversely subhexagonal, the front is entire and the anterolateral margins are thin, with two blunt spines, the posterior one at the lateral angle weakly ridged; with or without a low ridge across the posterior part of the mesogastric lobe. Chelipeds subequal; the upper margin of the hand is carinate, with blunt spines or granules and there are three longitudinal ridges on the outer margin of the hand.

Remarks. While close to *Palaeocarpilius*, *Proxicarpilius* differs in having shorter second antennal segments, the front is straighter and more distinctly divided into median and lateral portions flanked by fairly robust inner orbital spines; the lateral angle occurs closer to the front producing shorter anterolateral margins which are less regularly convex, and the branchial region is not deflected beneath an epibranchial ridge. The longitudinal ridges on the outer margin of the hand distinguish those of *Proxicarpilius* from *Palaeocarpilius.*

Proxicarpilius planifrons sp. nov.

Plate 117, figs. 5, 7; Plate 118, figs. 1–4, 7

Derivation of name. The trivial name refers to the entire, i.e. notchless front.

Diagnosis. A *Proxicarpilius* with a transverse ridge across the posterior part of the mesogastric lobe; the lowermost carina on the hand is discontinuous.

Material. One hundred and eighty-four carapaces and six unattached chelipeds. Holotype, an almost entire female carapace and part of left cheliped, In. 61575. Paratypes, 75 males, In. 61576–61599; 42 females, In. 61600–61619; 66 of indeterminate sex, In. 61620–61640, and 6 unattached chelipeds, In. 61641–61646.

Horizon and locality. Middle Eocene, Kirthar Formation, Domanda Shale, Ramak Kwar, *c.* 85 km southwest of Dera Ismail Khan, North West Frontier Province.

Description. The carapace is subhexagonal in outline, the length being about three-fourths the width measured between the lateral spines. It is moderately arched transversely and steeply rounded in longitudinal section. There is a blunt spine a little more

than half-way along the broadly rounded anterolateral margin, and another larger one at the anterolateral angle set two-thirds distant from the front. There is a suggestion of an epibranchial ridge so prominently developed in *Palaeocarpilius*. The edge is narrowly rounded, slightly upturned, and the sides are inclined under at about 45°. The posterolateral margins are sinuous and converge to fairly sharp angles leading by slight excavations from the 5th coxae into the almost straight posterior margin which is bounded by a thin marginal groove and is about twice as wide as the front. The orbits are broadly ovate, directed forwards, and take up the outer fourths of the orbitofrontal margin which is very wide, occupying about three-fourths of the carapace width. The upper orbital margin is sinuous towards the front and thickened by a rounded ridge, which becoming much thinner, continues across the front. The inner upper orbital spine is blunt and a little weaker than the outer one.

The suborbital spine is visible from above and the 2nd segment of the antenna completes the thin lower margin of the orbit. The front is divided into three parts; the lateral portions are concave, and the central wider portion is broadly convex with no trace of a median notch, depressed and barely projected beyond the inner upper orbital spines. The lobes are moderately well defined. A narrow, gently curving ridge extends across the posterior part of the mesogastric lobe and a small ovate node on each protogastric lobe overlays the extremities of the 'epigastric ridge'. As growth advances there is a tendency for these nodes to extend forwards and inwards to enclose a shallow depression on either side of the mesogastric lobe. Continuing from the protogastric nodes is the first of a row of six or seven small tubercles curving outwards and backwards to the 'epibranchial ridge'. Anterior to the mesogastric ridge are two pits, rather more obvious on a subsurface shell-layer, close to the midline. The slightly tumid cardiac region is confluent with the urogastric lobe and with it forms an elongate pentagon with three small tubercles set in an inverted triangle on the broadest part. The intestinal region is ovate and barely distinguished posteriorly from the metabranchial lobes. Pits of several diameters crowd the gastric and cardiac regions. On the metabranchial lobes the pits are smaller and become almost obsolete posteriorly.

On the ventral surface the front curves downward and backward to meet the head of the very narrow epistome which has a thinly ridged margin. The basal segment of the antennules is semi-elliptical with the lower margin sinuous and ridged; when deflected to show the joint with its distal members, it is rectangular with the corners rounded. The second segment of the antenna is subtrapezoidal at its base with a short facet articulating with a notch on the subhepatic margin; the very narrow distal portion terminating in the orbit lays under the inner orbital spine for half its width. The corneal surface entirely caps the short, cylindrical eyestalk. A thin groove extends across the anterior margin of the endostome. The buccal margins converge a little posteriorly and the distal angles are broadly rounded; the margins are bounded by a thin ridge which continues round the sternal border. The ischio-endognath of the 3rd maxillipeds is rhomboidal with a rounded ridge on its outer third (Pl. 118, fig. 2). The merognath is subovate with the lower inner angle truncated; it has a thin median ridge flanked by broad depressions. The transversely rounded exognath is about two-thirds the width of the endognath. Fine pits are scattered over the antennular region and mouth parts.

The part of the sternum corresponding to the 1st/2nd abdominal sternites is triangular and emphasized by a strong median ridge and a curved basal ridge, which, interrupted only by shallow clefts, continues along the distal edge of the 3rd and lateral part of the 4th sternites; a weak transverse groove further delineates the 1st/2nd sternites from the 3rd, and between the 3rd and the 4th a broader groove curves nearly to the abdominal trough. The 4th sternites are very large and in the male (In. 61577) are divided by a ridge curving round the abdominal trough; the surface is steeply depressed forward of the ridge, and is flat behind; but in the female (In. 61602) this ridge broadens behind into tumidities and the depressed part is bilaterally tumid. The 5th/8th sternites are chordate in outline.

The 2nd abdominal somite of the male is about half as long again as the 1st; the 3rd–5th are fused (Pl. 118, fig. 3), but their positions are marked by marginal notches and short median and lateral grooves. The 6th somite is rectangular and about two-thirds the length of the triangular telson; the 3rd is the widest and the 2nd–5th have a progressively weakening transverse ridge. The middle third of each somite is weakly tumid. In the female abdomen the lower margin of the 1st somite is medially about half the length of the 2nd; the 3rd–5th become slightly longer, and the 6th is widest and about twice the length of the 5th and half that of the subovate telson; the median and lateral portions are tumid. The openings of the oviducts (Pl. 118, fig. 4) are large and occur between the 5th–6th sternites.

In the female the percentage ratio of the posterior margin to carapace width averages 30·3, while in the male it is 26·9, a difference of 11·5%.

The chelipeds are robust and the larger claw, where preserved, is on the right. The merus is triangular with a fairly sharp lower margin on which there are two blunt spines in line distally, the larger forming the articulating boss with the carpus. The carpus is a little shorter than the merus, triangular in section, with a row of five or six blunt spines fringing the upper outer margin. The length of the slightly incurved major palm is a little more than twice the carpus and the inner surface is smooth; the upper margin is sharp, finely granulated, and terminates distally in a sharp spine; on the outer surface are three subparallel ridges strengthening distally; the bluntly rounded uppermost commences posteriorly at the upper articulating boss, the lowermost is 'broken' with the centre portion laying nearer the middle ridge. The lower

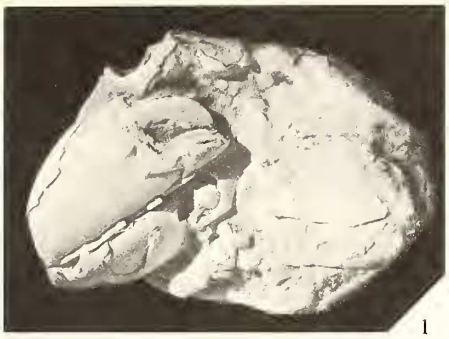
EXPLANATION OF PLATE 118

Figs. 1–4, 7. *Proxicarpilius planifrons* gen. et sp. nov. Middle Eocene, Kirthar Formation; Ramak Kwar. 1, ventral view of female carapace to show right cheliped, BM In. 61600, ×2. 2, antero-ventral view of carapace, BM In. 61601, ×2. 3, ventral view of male carapace, BM In. 61576, ×2. 4, ventral view of female carapace to show oviducts, BM In. 61602, ×2. 7, right lateral view of holotype carapace, BM In. 61575, ×2.

Figs. 5, 6, 11. *Proxicarpilius minor* gen. et sp. nov. Middle Eocene, Kirthar Formation; Parwara. 5, outer face of right chela, BM In. 61656, ×3. 6, outer face of left chela, BM In. 61657, ×3. 11, right lateral view of holotype carapace, BM In. 61647, ×3.

Figs. 8–10, 12. *Hexapus pinfoldi* sp. nov. Middle Eocene, Kirthar Formation; Parwara. 8, ventral view of male carapace, BM In. 61661, ×3. 9, 10, 12, dorsal, left lateral, and ventral view of the holotype female carapace, BM In. 61660, ×3.

Figs. 13–15. *Glyphithyreus wetherelli* (Bell), Palaeocene, Upper Ranikot Formation; Kalabagh. Dorsal, ventral, and right lateral views of carapace, BM In. 48194, ×2.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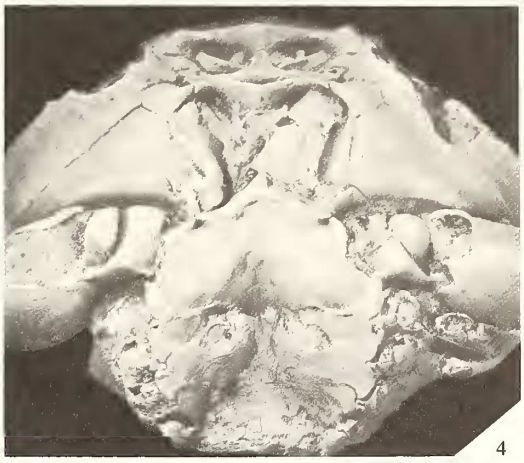
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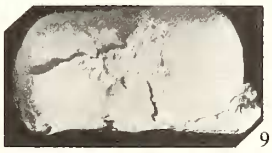
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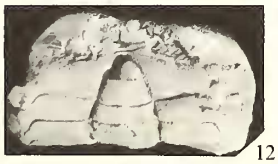
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COLLINS and MORRIS, Lower Tertiary Crabs

margin is straight and bordered on the outer surface by a groove continuing along the fixed finger, which is about half the length of the palm; on the opposing margin is a large tooth before the terminal one. The opposing margin of the fixed finger is narrowly rounded. Minute granules crowd the surface of the carpus and merus; on the palm the outer surface down to the lowest ridge is granulated, the granules becoming finer, fewer, and interspersed with pits towards the lower margin. The chelipeds appear to be rather more robust in the males. The tips of the fingers retain the dark coloration typical of the Carpiliidae and other members of the Xanthoidea.

Discussion. In *Palaeocarpilius*, only *P. simplex* Stoliczka and *P. klipsteini* von Meyer have an entire front edge, but the front itself is subtriangular rather than broadly rounded as in *P. planifrons*. Both these species of *Palaeocarpilius* have a smoothly convex anterolateral margin and whereas the upper margin of the hand of *P. simplex* is smooth and that of *P. klipsteini* is tuberculate, neither has the longitudinal ridges on the outer margin like those developed in *Proxicarpilius*.

Proxicarpilius minor sp. nov.

Plate 117, figs. 6, 8, 9; Plate 118, figs. 5, 6, 11

Derivation of name. From the generally small size of the available specimens.

Diagnosis. A *Proxicarpilius* with a smooth dorsal surface lacking a transverse gastric ridge; on the cheliped the lowermost carina on the hand is entire and the upper and lower margins are coarsely granulate.

Material. Holotype, an almost entire carapace, In. 61647. Paratypes, eight carapaces and four attributed chelipeds, In. 61648-61659.

Horizon and locality. Middle Eocene, lower part of Drazinda Shale, Kirthar Formation, *c.* 150 m below top, near axis of Parwara Syncline, south of Parwara village, 9 km south-west of Domanda, Dera Ismail Khan district, North West Frontier Province, Pakistan, 31° 32′ N., 70° 9′ E.

Description. The specimens are of small size, ranging from 11 to 19·5 mm in width. In general outline they closely resemble similar-sized specimens of *P. planifrons*, but the length/width ratio of *P. minor* is just perceptably less than that of *P. planifrons*. Four specimens each of the two species were measured and their average percentage ratios were 71% for *P. minor* and 77% for *P. planifrons*. Of greater specific significance is that the dorsal surface of *P. minor* is less convex longitudinally, the lobes are undifferentiated and no transverse ridge is developed across the mesogastric lobe.

Four chelae present in the Drazinda Shale collection, show close affinity to those of *P. planifrons* and may be regarded as belonging to *P. minor*; the upper margin of the hand is bluntly rounded with four evenly spaced spinules; five or six spinules line the outer lower margin and are alternately spaced with a similar number of spinules on the inner margin. The three carinae on the outer margin are weakly developed and the lowermost is uninterrupted in the centre.

Family GONEPLACIDAE McLeay, 1838
Subfamily HEXAPODINAE Miers, 1886
Genus HEXAPUS de Haan, 1833

Type species. Cancer sexpes Fabricius, 1798 by original designation.

Range. Middle Eocene to Recent.

Hexapus pinfoldi sp. nov.

Plate 118, figs. 8–10, 12

Derivation of name. In honour of E. S. Pinfold.

Diagnosis. The carapace is subrectangular in outline with short, rounded, anterolateral margins and subparallel lateral margins; the regions are indistinct.

Material. Eight, part cast, part decorticated carapaces. Holotype, female, In. 61660. Paratypes, 3 males, In. 61661–61663; 2 females, In. 61664–61665, 2 of indeterminate sex, In. 61666–61667.

Horizon and locality. Middle Eocene, Kirthar Formation, lower part of Drazinda Shale, *c.* 150 m below top, near axis of Parwara Syncline, south of Parwara village, 9 km south-west of Domanda, Dera Ismail Khan district, North West Frontier Province, Pakistan, 31° 32′ N., 70° 09′ E.

Description. The carapace is subrectangular in outline, the length being a little more than half the width; it is steeply arched longitudinally, particularly anteriorly, and transversely is nearly flat. The anterolateral margin is very short and rounded smoothly into the orbitofrontal margin which is straight and occupies about one-third of the carapace width. The posterolateral margins are gently convex to subparallel and the posterolateral angles are fairly sharp. The posterior margin is vaguely divided into three parts, the outer parts concave and the middle convex. A finely granulated ridge extends just below the very slightly rounded lateral edges and the weakly tumid sides are inclined almost at right angles. The orbits are ovate and the scarcely raised upper orbital margin is thin and not so far advanced as the lower orbital margin which terminates in a small node. The eyestalk is cylindrical with a median constriction and the corneal area caps the extremity. The front is not well preserved in any of the specimens, but appears to have occupied about one-fifth of the carapace width. The regions are indistinct. Faint gastrocardiac grooves extend over the middle fifth of the carapace length; they are set apart equal to the distance between the orbits and between them are two pits close to the midline. The dorsal surface and sides are finely granulated.

The pterygostomian regions are short and triangular, somewhat tumid, and tending to overlap the anterior sternites. The buccal angle is broadly rounded and distally chamfered to accommodate the chelipeds. The buccal margins are a little divergent posteriorly and bounded by a finely granulated ridge.

A deep forwardly curved groove separates the 3rd from the 4th sternites, it does not reach the side but stops at a slot in the anterior margin. The 4th sternites are about twice the length of the 5th–7th; these are subrectangular in outline with sharp inner anterior angles and rounded posterior ones; the margin of the 5th and 6th is drawn back laterally to embrace half each succeeding sternite. A few small granules occur on the outer anterior angles of the 4th sternites and the remaining surface appears

to have been finely pitted. The abdominal somites of the male are narrow and of about equal length, they taper gradually to the bluntly rounded telson. The female abdomen is ovate, reaching its widest part at the 4th–6th somites which are of about equal length; the triangular telson is a little longer than the 6th somite and its apex is broadly rounded.

Discussion. Two members of the Hexapodinae, *Goniocypoda rajasthanica* Glaessner and Rao and *G. sindensis* Glaessner have already been described from the Indian Sub-Continent; the former comes from the Fuller's Earth deposits (Upper Palaeocene to Lower Eocene) of Rajasthan, and the latter is possibly of Eocene age from Sind (Sastry and Mathur, 1970). In both these species the orbitofrontal margin is very broad and sharply in contrast with that of *H. pinfoldi*. The only other known fossil *Hexapus* is *H. nakajimai* Imaizumi from the Miocene Nakajima formation of Japan; it differs from *H. pinfoldi* in having rather more prominent gastrocardiac grooves, and the anterior process of the mesogastric lobe is markedly depressed. *H. sexpes* (Fabricius) a Recent species occurring off Japan, New Caledonia, Amboina, and South Africa, has weakly developed gastrocardiac grooves, but the posterolateral margins are somewhat divergent to the posterior margin, rather than subparallel as in *H. pinfoldi*.

The relative size of the pereiopods and details of the front distinguish *Hexapus* from *Thaumastoplax* (Sakai, 1939; Glaessner, 1969). In drawing attention to the difficulty of collecting fossil crabs retaining these characters, *Imaizumi* (1959) introduced a biometric evaluation for *Hexapus* and *Thaumastoplax* based on the ratio of the carapace length to width. Ratios, shown by a common denominator of the two species of *Hexapus* known to Imaizumi were, 637/1092 for *H. sexpes* and 624/1092 for *H. nakajimai*, and for the three species of *Thaumastoplax* available to Imaizumi: 756/1092 for *T. orientalis* Rathbun; 672/1092 for *T. anomalipes* Miers (both Recent); and 728/1092 for *T. prima* Rathbun (Oligocene). Measurements taken from Wood's illustration of *T. eocenica*, provide us with a figure of 756/1092. Only three specimens of *H. pinfoldi* are sufficiently well preserved to permit measurements to be taken. Ratios of the figures obtained shown in Imaizumi's common denominator, are: 651/1092, 640/1092, and 632/1092, which provide an average of 641/1092. While this is a little higher than the figures shown for the other members of *Hexapus*, it is still lower than the lowest figure obtained in *Thaumastoplax*, i.e. *T. anomalipes*.

Measurements of *T. intermedia* Collins and Morris (Miocene) are length 14·4 mm and width 22·0 mm which reduce to 702/1092, showing that the species falls well within the general range provided by other members of the genus and supplements our remarks (1976) concerning that species' affinity to both *T. prima* and *T. anomalipes*.

Subfamily CARCINOPLACINAE H. Milne-Edwards, 1852
Genus GLYPHITHYREUS Reuss, 1859

Type species. Glyphithyreus formosus Reuss, 1859 by original designation.

Range. Palaeocene to Eocene.

Glyphithyreus wetherelli (Bell)

Plate 118, figs. 13–15

1858 *Plagiolophus wetherelli* Bell, p. 19, pl. 7, figs. 7–13.
1859 *Glyphithyreus affinis* Reuss, p. 5, pl. 10, figs. 4, 5.
1937 *Plagiolophus* cf. *wetherelli* (Bell); Pinfold, p. 9.
1954 *Clyphithyreus* [*sic*] *wetherelli* (Bell); Brown and Castell, p. 63.
1969 *Glyphithyreus wetherelli* (Bell); Via, p. 302, pl. 36, fig. 1 (see also for intermediate synonymies).

Material. Twenty-one part cast, part decorticated carapaces: In. 48194. Palaeocene, Upper Ranikot Formation, Patala Shale, 2 miles north of Kalabagh, Punjab; In. 48232–48237, top of Ghazij Formation, Shaisuro, Dera Ghazi Khan, Punjab; In. 49188–49201, Ghazij Formation, Kalchis, Baluchistan.

Remarks. The specimens range in size from 15·6 to 34·2 mm in carapace width, thus attaining a larger size than is usual for European forms. A series of length/width

TABLE 2. Measurements (mm) of specimens of *G. wetherelli*, *G. affinus*, and *G. formosus* from various localities, with their percentage length/width ratios.

	length	*width*	*l*/*w*%
Glythithyreus wetherelli (Bell)			
Pakistan	22·9	28·5	83·4
(Pinfold Colln.)	20·2	27·0	74·9
	26·5	34·2	74·6
	22·3	26·9	82·9
	12·9	15·6	82·7
(T. O. Morris Colln.)	16·8	22·3	75·3
	19·7	24·1	81·7
	22·5	27·7	81·2
Sheppey (Bell, 1858; 20)	22·6	27·7	81·5
Sheppey	14·8	19·0	77·9
	14·6	18·8	77·7
	14·0	18·0	77·8
	9·5	12·5	76·0
Oxshott	14·9	18·8	79·3
	14·6	18·8	77·7
Senegal (from Remy, 1954; pl. 11, fig. 3)	16·0	21·0	76·0
Spain (from Via, 1969; 303)	20·0	26·0	77·0
Glythithyreus affinis Reuss			
Sheppey (from Reuss, 1859; pl. 10, fig. 4)	14·9	20·0	74·5
Glythithyreus formosus Reuss			
Germany (from Reuss, 1859; pl. 2, fig. 3)	16·0	25·0	64·0

ratios compares favourably with well-preserved London Clay specimens from Sheppey, Kent, and Oxshott, Surrey. Similarly the figures shown by Via (1969, p. 303) for the specimen from the Ypresian of Spain, together with measurements taken from the figure of Remy's (1954) specimen from Senegal also agree and appear to fall into two groups, 74–77 and 79–83;—this difference may be accounted for by sexual dimorphism.

Size for size there is close similarity of surface areolation, but in the larger Ghazij specimens the metabranchial lobes progress from the generally bar-like ridges of Sheppey forms to larger, rounded lobes with a subsequent shallower depression between them and the mesobranchial lobes. Larger specimens from Oxshott, Surrey, which are exposed in a stratigraphically higher London Clay Zone (Wrigley's Bed 5) than at Sheppey, show the metabranchial lobe to be expanding towards the development attained by the Ghazij specimens. The specimen from the Upper Ranikot (Thanetian) is the earliest representative of this species, which elsewhere, i.e. England, Belgium, Denmark, Spain, and Senegal, does not occur until the Ypresian. The absence of this species from these other countries does not necessarily imply a westerly migration, since beds of Thanetian age seldom preserve crabs except as rare indeterminate fragments of fingers.

The figures, of the Cretaceous (?Cenomanian) species *G. formosus* published by Reuss (1859) and Milne-Edwards (1865), are of the same specimen and for which the length-breadth percentage ratio of 64 was obtained; considerably lower than the ratios for *G. wetherelli*; there are also distinct differences in surface areolation indicating that *G. formosus* is a valid species.

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